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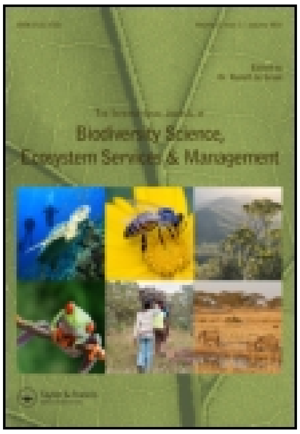

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To assess future interactions between the environment and human well-being, spatially explicit ecosystem service models are needed. Currently available models mainly focus on provisioning services and do not distinguish changes in the functioning of the ecosystem (Ecosystem Functions – ESFs) and human use of such functions (Ecosystem Services – ESSs). This limits the insight on the impact of global change on human well-being. We present a set of models for assessing ESFs and ESSs. We mapped a diverse set of provisioning, regulating and cultural services, focusing on services that depend on the landscape structure. Services were mapped using global-scale data sets. We evaluated the models for a sample area comprising Eastern Europe. ESFs are mainly available in natural areas, while hotspots of ESS supply are found in areas with heterogeneous land cover. Here, natural land cover where ESFs are available is mixed with areas where the ESSs are utilized. We conclude that spatial patterns of several ESFs and ESSs can be mapped at global scale using existing global-scale data sets. As land-cover change has different impacts on different aspects of the interaction between humans and the environment, it is essential to clearly distinguish between ESFs and ESSs in integrated assessment studies.

Keywords: global scale; natural hazard protection; pollination; crop yield; wild food; carbon sequestration; tourism; air quality

Introduction

Over the past centuries, human activities have considerably altered the Earth's surface. Between the years 1500 and 2000, the global population increased from 295 to 6145 million. The population increase was accompanied by a 6-fold increase of the cropland area and a 15-fold increase of the pasture area (Klein Goldewijk et al. 2011), mostly at the expense of forest and natural rangeland areas. These land-cover changes have altered atmospheric CO_2 concentrations (Houghton 1999), climate (Ruddiman 2003) and erosion rates (Wilkinson and McElroy 2007; Zalasiewicz et al. 2008) and led to the decline and extinction of plant and animal species (Mace et al. 2005; Butchart et al. 2010). Human impact on the Earth's surface is regarded as the dominant process controlling the Earth system since several millennia (Crutzen and Steffen 2003; Ruddiman 2003; Zalasiewicz et al. 2008).

Human impacts have resulted in degradation of the capacity of some of the Earth's ecosystems to provide goods and services that are essential for human well-being. According to scenario analyses, human impact on natural systems will increase the next decennia, and further degradation of ecosystems is expected (MA 2005; Intergovernmental Panel on Climate Change 2007; United Nations 2011). To ensure future provision of ecosystem goods and services under the expected future population and climate changes, the Conference of Parties to the Convention of Biological Diversity (COP CBD) adapted targets to prevent further degradation of biodiversity and ecosystems (United Nations Environment Programme Convention on Biological Diversity 2010). To underpin and to evaluate these targets, relationships between properties of the ecosystem, for example, biodiversity, the ecological functions they perform and the services they provide to humans should be quantified. Because of spatial differences of the impact of global change, spatially explicit information on changes of ecosystem functioning is essential to inform decision-making and policy formulation.

Several attempts to provide quantitative information on ecosystem service provision exist. The Millennium Ecosystem Assessment (MA) was important in defining and quantifying ecosystem services (ESSs) at global scale (MA 2005). Mapping ESSs is more recent and some authors achieved to map a limited set of ESSs at global scale (Turner et al. 2007; Naidoo et al. 2008) or regional and local scales (Chan et al. 2006; Egoh et al. 2008; Nelson et al. 2009). To facilitate the analysis of ESSs, several tools have been developed, including InVest (Tallis et al. 2008), ARIES (Villa 2009) and GUMBO (Boumans et al. 2002). Despite the progress achieved in the last years, several issues remain to be developed.

First, there is no consensus on the definitions of services provided by ecosystems. The subdivision of ESSs in categories converges towards distinguishing categories of provisioning services, such as food and water; regulating services, such as air quality regulation; and cultural

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services, such as tourism (Lamarque et al. 2011). A recent framework made a subdivision between ecosystem functions (ESFs; the capacity of an ecosystem to deliver a service) and ESSs (the actual use of ESFs by humans and the contribution of the ecosystem to human well-being) (De Groot RS, Alkemade R, et al. 2010). Mapping and quantification exercises, however, tend to report jointly on ESFs and ESSs or only focus on ESFs (Willemen et al. 2008; Kienast et al. 2009), potentially leading to misinterpretation of the results (Lamarque et al. 2011). There are no studies yet that apply the function–services framework in a spatially explicit way.

Second, most studies only provide information on a limited subset of ESFs and ESSs (Seppelt et al. 2011), and especially at global level the focus tends to be on provisioning services and carbon sequestration. Third, studies or models for ESSs either cover a small area (O'Farrell et al. 2010; Egoh et al. 2011) or are not spatially explicit (Costanza et al. 1997; Alcamo et al. 2005; MA 2005). Finally, the effects of spatial and biophysical structure of the landscape, important for erosion and pollination among others (Steffan-Dewenter and Tscharntke 1999; Buis and Veldkamp 2008), and the effects of soil and climate are often overlooked (Kienast et al. 2009).

We present a methodology to map, quantify and simulate ESFs and ESSs. The methodology is closely linked to the IMAGE framework (Bouwman et al. 2006) and uses several inputs and outputs of the IMAGE framework. For this analysis we adopt the cascade approach where ecosystem properties determine ecological functions, that is, the capacity of supplying ESSs, and ESSs include the extent of the human use of ecosystems and can be regarded as the link between ecosystem functioning and human well-being (Haines-Young 2009; De Groot RS, Alkemade R, et al. 2010; De Groot R, Fisher B, et al. 2010). We based our analysis on global-scale data and evaluated the methodology through a study for Eastern Europe. Our main focus is to include many divergent ESSs, covering services that depend on the land-cover structure (Lamarque et al. 2011) and soil, climate and landscape. Spatial patterns of these functions and services are compared with the provisioning service of food.

Methods

Case study

We mapped a set of ESFs and ESSs in the year 2000 based on IMAGE simulations and global-scale data (Table 1). IMAGE is an integrated environmental assessment model framework that simulates the environmental consequences of human activities worldwide. It represents interactions between society, the biosphere and the

Table 1. Overview of the data used in this study.

Ecosystem property	Unit	Description	Source
Land cover		GlobCover global land cover map at a 250 m resolution	Bicheron et al. (2008)
Elevation	m	Gtopo30 global DEM at 1km resolution	GLOBE Task Team et al. (1999)
Precipitation sum	mm	Annual precipitation sum, 0.5° resolution	Bouwman et al. (2006)
Precipitation surplus	mm	Annual precipitation sum minus annual evapotranspiration, 0.5° resolution	Bouwman et al. (2006)
Precipitation distribution	%	% of annual precipitation per month, 0.5° resolution	CRU, Mitchell and Jones (2005); Bouwman et al. (2006)
Wet day frequency	#	Number of rain days per year	CRU, Mitchell and Jones (2005)
Temperature	°C	Annual mean temperature, 0.5° resolution	Bouwman et al. (2006)
Rivers		Location and hierarchy of rivers	US Geological Survey Earth Resources Observation and Science (1993)
Coasts		Land-sea boundary	ESRI
Soil characteristics	%, cm, g/cm^3	Clay, silt and sand content; rooting depth, bulk density, from the Harmonized World Soil Database version 1.0, at 30" resolution	FAO et al. (2008)
Human drivers			
Population density	#/km^2	Number of people per pixel at 1 arc second resolution	Oak Ridge National Laboratory (2005)
Crop fraction	%	For each crop included in IMAGE, the percentage of agricultural land in each IMAGE grid cell covered by this particular crop. Crops included are: Cereals (temperate/tropical), rice, maize, pulses, roots and tubers, oil crops	Bouwman et al. (2006)
GDP	€/capita	Gross Domestic Product per country and NUTS2 region	Eurostat (2011); UNstats (2011)
Roads		Location and type of roads, from GRIP	PBL Netherlands Environmental Assessment Agency (2010)
Management factor	–	Management intensity (IMAGE); crop specific and region specific	Bouwman et al. (2006)

Notes: DEM, Digital Elevation Model; GRIP, Global Road Inventory Project.

climate system to assess sustainability issues like climate change, biodiversity and human well-being. The objective of IMAGE is to explore the long-term dynamics of global change as a result of interacting demographic, technological, economic, social, cultural and political factors (Bouwman et al. 2006). The year 2000 was chosen because of the availability of a temporally consistent data set. Although the models are based on global-scale data, we present results for Eastern Europe (Figure 1). We selected a case study where no data specific to the area were available. Thereby, no studies on ESFs and ESSs exist for most of the areas of Eastern Europe (Seppelt et al. 2011) and Eastern Europe covers a wide range of land-cover, climate, soil and socio-economic conditions. Therefore, we consider Eastern Europe a suitable sample area for model development and testing.

Mapping ecosystem functions and services

For each service, a conceptual model of the relationship between ecosystem properties and the ESF was developed based on published equations or data, including online databases. ESSs were derived from ESFs by including the use of ESFs by humans in the model (Figure 2). For this, the demand of the function has been quantified, by, for example, calculating the yield of crops that depend on animal pollinators or the fraction of the land where human use requires protection against erosion or floods. An overview of the data used in this study is presented in Table 1. For each ESF and ESS model, spatial calculations were done at the input resolution of the ecosystem property data (Table 1) and aggregated to 0.5° × 0.5° grid cells by calculating an area-weighted average value over each output grid cell. We simulated the provisioning services, such as food crop yield; regulating services, such as carbon sequestration, protection against natural hazards including erosion and floods, pollination and air quality; cultural services, such as tourism; and the provision of wild food which is both a cultural and a provisioning service (MA 2005).

Food crop yield

Food crop yield (Mg/km^2 per growth cycle in fresh weight) was simulated with the IMAGE framework (Bouwman et al. 2006). The ESF for food crop yield was defined as the potential yield a location can provide, that is, the maximum of the potential yields of all crops included in IMAGE (Table 1). Potential yields were calculated as a function of climate, soil and relief conditions. The ESS for food crop yield was the actual yield. This was calculated from the potential yield by including the actual crop cover and the management factor (Table 1).

Wild food

Collection of wild food can provide an important part of the diet and can be seen as a sport or be important in local traditions (Russell 2007). The ESF for wild food was defined as the annual availability of game, fish, berries and mushrooms (kg/km^2). Based on the national and international hunting statistics (European Forest Institute 2007; FAO 2011), average availability of game, fish, berries and mushrooms per square kilometre for each land-cover type was calculated and coupled to the land-cover map. The ESS for wild food was calculated as the amount of wild food accessible to people within the maximum amount of time that people spend for collecting wild food. In this study, for game, a threshold of 2 hours was assumed; for fish 1 hour and for mushrooms and berry collection 0.5 hours (de Roman and Boa 2004; US Dept IFWS et al. 2006; Tsachalidis and Hadjisterkotis 2008; Schunko and Vogl 2010). Travel time from villages was calculated by applying the methods described by Nelson (2008) to the data described in Table 1.

Carbon sequestration

Sequestration of carbon in soil and vegetation is seen as a means for mitigating climate change (United Nations Framework Convention on Climate Change 1997). The ESF for carbon sequestration was defined as the net ecosystem productivity (NEP) (Mg C/km^2 per year),

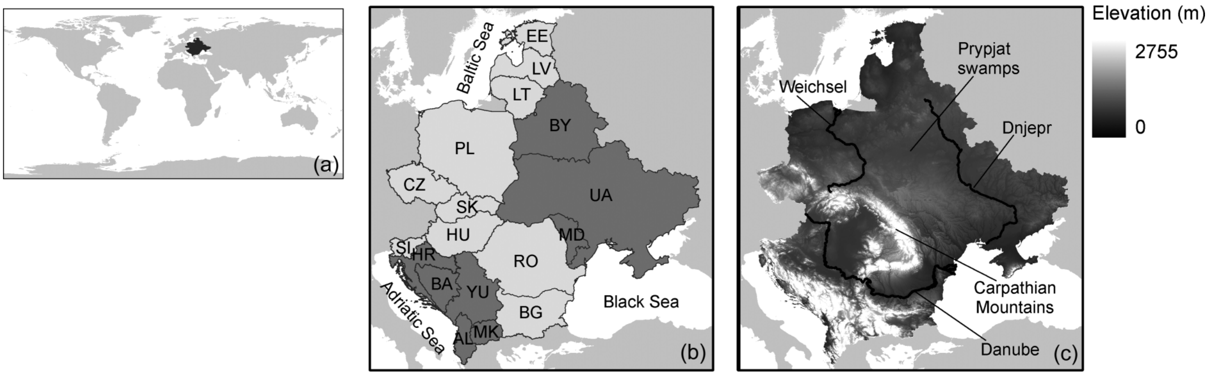

Figure 1. (a) Location of the sample area on the globe. (b) General topography of the sample area. The light grey countries are member of the European Union (EU). (c) Main geographical features of the sample area.
Notes: EE, Estonia; LV, Latvia; LT, Lithuania; BY, Belarus; PL, Poland; CZ, Czech Republic; SK, Slovakia; HU, Hungary; SL, Slovenia; HR, Croatia; BA, Bosnia-Herzegovina; YU, Serbia-Montenegro; AL, Albania; MK, Macedonia; BG, Bulgaria; RO, Rumania; MD, Moldova; UA, Ukraine.

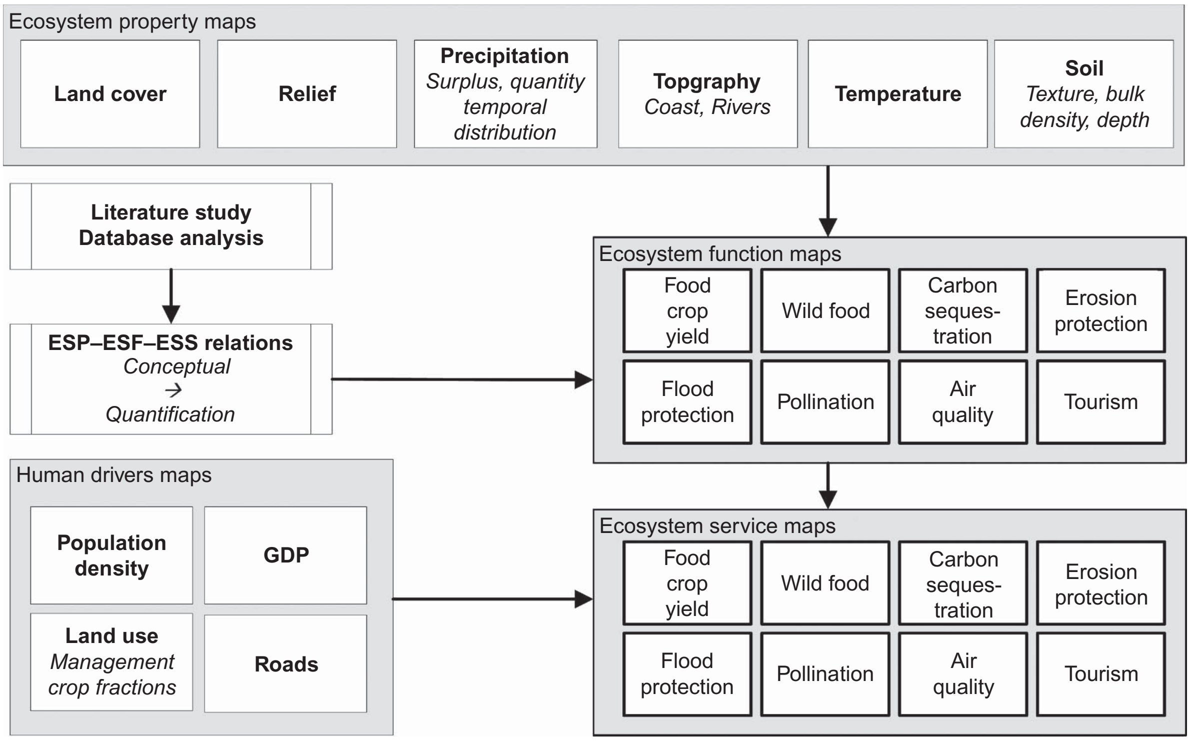

Figure 2. Overview of the methodology.

which is the difference between net primary productivity (NPP) and respiration, which have both been simulated with the IMAGE framework (Bouwman et al. 2006). NPP was considered a function of climate, soil, atmospheric CO_2 concentration, altitude, land cover and land-cover history. Respiration depends on the carbon stocks in different soil compartments, turnover rates, soil water availability and temperature. The ESS for carbon sequestration was defined as the climate regulation by capturing CO_2 in soil and vegetation and calculated as the percentage of the annual country total CO_2 emission (UNstats 2011) that is captured by the ecosystem.

Protection against erosion

We calculated the erosion protection ESF as the decrease of erosion risk by vegetation, using indices ranging from 0 to 1 for the protective effects of each land-cover type as provided by Hootsmans et al. (2001). The ESS for erosion protection was defined as the decrease of erosion risk by vegetation in utilized areas with a high erosion risk. Erosion risk due to soil and landscape characteristics and rainfall intensity was mapped using a 0–1 index based on the Universal Soil Loss Equation (USLE) (Batjes 1996). To calculate the ESS for erosion protection, the erosion risk index was multiplied with data from the erosion ESF map (Batjes 1996). Utilized areas are croplands and urban areas and were defined using the land-cover map (Table 1).

Flood protection

Floods can occur due to accumulation of run-off, river flooding or flooding from the sea while vegetation cover and soils can retain run-off and thus protect against floods (Fohrer et al. 2005). To map the ESF for flood protection, first, the retention capacity of the landscape (%) was calculated, using retention capacities as a function of land cover (Johnston et al. 1990; Fernández et al. 1996; Brye et al. 2000) and soil (FAO et al. 2008) and maps of land cover and soil characteristics (Table 1). Then, sensitive areas, defined as areas close to rivers or coasts with a low elevation difference with the river or coast, or areas that receive a lot of run-off were mapped. Third, the ESF was calculated as the retention capacity in areas that are sensitive to floods. Finally, the ESS for flood risk (percentage of grid cell with flood risk) was calculated as the ESF in areas that are sensitive to floods due to utilization of the land for crop production and urban land (Table 1).

Pollination

Several food crops depend on animal pollinators for pollination (Gallai et al. 2009). The pollination ESF was defined as the percentage yield loss due to diminished pollination (yield reduction fraction – YRF). In this study, the YRF was calculated for pulses and oil crops only. Other crops that dependent on pollinators are not included in the IMAGE model. For the pollinator-dependent crops, the YRF is set at 100% at a zero distance to nature and decreases upon increasing distance to nature. At a distance to nature >1200 m, the YRF is 40% (Steffan-Dewenter and Tscharntke 1999; Klein et al. 2007; Schulp and Alkemade 2011). The ESS for pollination was calculated as the additional yield (Mg/km^2) of pulses and oil crops due to wild pollination, based on the YRF and the food crop yield (Section *Food crop yield*).

Air quality

As ESF for air quality, we calculated the capacity of the landscape to capture dust particles <10 μm (PM_{10}) (%). Atmospheric PM_{10} concentrations are influenced by vegetation that captures PM_{10}, rainfall and temperature (Fischer et al. 2004; Anttila and Salmi 2006). The percentage captured by vegetation was derived from Oosterbaan et al. (2009) and Pace (2003). The percentage PM_{10} removed from the atmosphere due to precipitation and temperature was calculated based on PM_{10} concentrations in 2000 from air quality monitoring stations throughout Europe (European Environment Agency 2011) and weather characteristics at the monitoring locations derived from the data described in Table 1. The ESS for air quality was considered as the amount of PM_{10} actually captured (g/km^2). This was calculated by multiplying atmospheric PM_{10} concentrations for Pan-Europe (Centre on Emission Inventories and Projections 2011) with the ESF for air quality.

Tourism and recreation

The ESF for tourism was defined as the capacity of landscapes to supply attractive areas for tourism and recreation. We estimated indices for the attractiveness based on landscape features attractive for tourists and holidaymakers. Each index ranges from 0 (unattractive) to 1 (attractive). Landscape features included were the presence of coasts, relief (low mountainous areas are attractive), land cover (varied land cover, with low amounts of urban area and arable land are particularly attractive) and the presence of protected natural areas (Hall 1998; Russell 2007; Willemen et al. 2008; Kienast et al. 2009). The indices were quantified using the data described in Table 1 and the data from Eurostat (2011). Finally, an average index was calculated.

The ESS for tourism was defined as the suitability of attractive areas. People spend more time for holiday and recreation in richer regions (Nowaczek and Fennel 2002) and areas need to be accessible to attract tourists or holidaymakers. To map the tourism ESS, therefore, the tourism ESF was supplemented with an index for GDP and the accessible areas were identified using the travel time map (Section *Wild food*).

Combining services and visual presentation

To interpret the results and demonstrate the spatial relationships between ESFs, ESSs and landscape characteristics, we calculated landscape characteristics (% nature, % agricultural land, number of land-cover types per 0.5° × 0.5° grid cell, degree of mixing of land-cover types) based on the land-cover map (Table 1). Then, correlations between ESFs, ESSs and the landscape characteristics were calculated. To assess the credibility of our models, we compared the model results with maps, data or literature that give an indication of the level of supply of the service. Data sources are described in Section *Comparison with other studies*.

All ESF and ESS maps were linearly normalized towards a 0–1 scale. Then, all normalized maps are added up and normalized again to provide a general overview of the availability of ESFs and supply of ESSs. The same was done for all categories (provisioning, regulating, cultural) separately. For the provisioning services, the non-normalized maps were added up and then normalized to give a realistic weight to the contribution of total food provision of both food crop production and wild food harvest.

Results

Ecosystem functions

Maps of all ESFs separately and added up are presented in Figure 3. For the provisioning functions (Figure 3a), Ukraine is a hotspot while low levels could be found in Estonia, eastern Hungary and along the Adriatic coast (Figure 1b). This pattern is strongly controlled by the potential crop yield, while the potential wild food yield is of lower importance (Figure 3e and f).

The availability of regulating functions (Figure 3b) is highest in the Carpathian and Adriatic Mountains while a lower level can be seen in Ukraine. This pattern applies for most regulating functions separately (Figure 3g–k). Flood protection, however, is available mostly close to rivers and the coast (Figure 3i). An exception is the region along the Danube (Figure 1c) in south-eastern Hungary and Romania, where the flood protection ESF is low despite a high river density.

The cultural functions show a pattern comparable with the regulating functions. For the tourism ESF, there are few small areas with a high availability while in most of the areas in Eastern Europe we expect low ESF availability.

Altogether, the Baltic countries, the Carpathian Mountains and the Adriatic region are hotspots for ESF availability. ESF availability is lower in Eastern Hungary, central Poland and the lower Danube region (Figure 3d). Hotspots of provisioning functions and hotspots of other functions hardly overlap, as illustrated by the negative correlations between provisioning and other functions ($r = -0.24$ with cultural ESFs and $r = -0.18$ with regulating ESFs). Cultural and regulating functions overlap to a large extent ($r = 0.78$) with high availability in the Carpathian Mountains (Figure 3b and c).

The availability of provisioning functions is positively correlated with the percentage agriculture (Table 2). The highest availability of provisioning functions is, however, seen in areas with a mixed land cover dominated by agricultural land (Figure 4). The availability of regulating and cultural functions is strongly positively correlated with the percentage of nature in the 0.5° × 0.5° grid cell (Table 2; Figure 4).

Ecosystem services

The supply of provisioning services (Figure 5a) is highest in the European Union (EU) member states (Figure 1b).

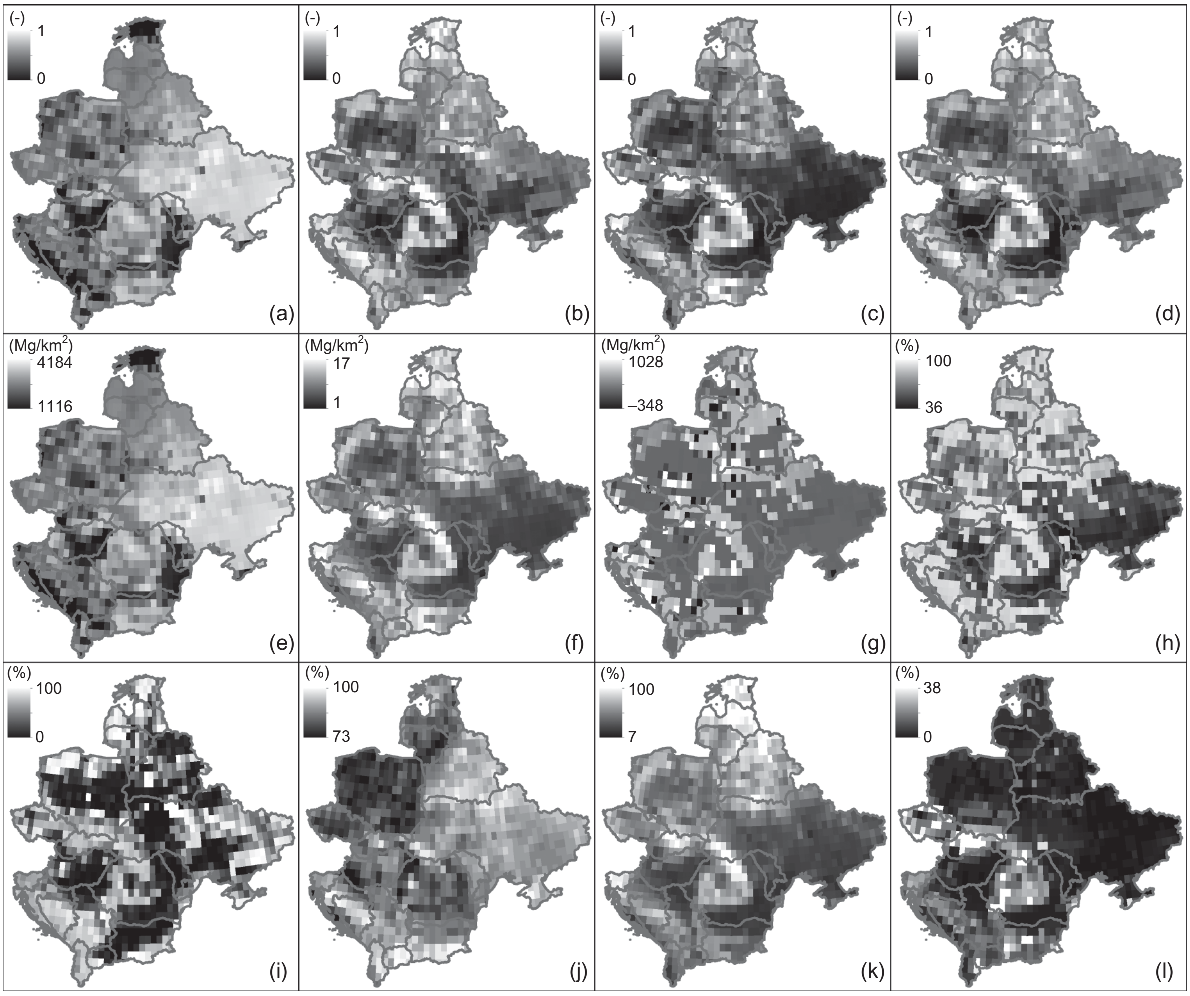

Figure 3. Availability of ecosystem functions in Eastern Europe. (a) Normalized sum of provisioning functions. (b) Normalized sum of regulating functions. (c) Normalized sum of cultural functions. (d) Normalized sum of all functions. (e) Potential food crop yield. (f) Wild food availability. (g) Carbon flux (positive is sequestration, negative is emission). (h) Erosion protection. (i) Flood protection. (j) Pollination yield reduction fraction. (k) PM_{10} capture capacity. (l) Landscape attractiveness for tourism.

Table 2. Correlation between availability of ESFs, supply of ESSs and landscape characteristics.

	Landscape characteristics of 0.5° × 0.5° grid cells		
ESF/ESS category	Number of land cover types	Agricultural land cover (%)	Natural land cover (%)
Functions			
All	0.34	−0.75	0.75
Provisioning	−0.16	0.19	−0.20
Regulating	0.37	−0.75	0.75
Cultural	0.33	−0.88	0.90
Services			
All	−0.03	0.16	−0.16
Provisioning	−0.19	0.36	−0.35
Regulating	0.04	0.45	−0.47
Cultural	0.32	−0.84	0.85

The spatial pattern is dominated by the food crop yield (Figure 5e). In most areas with crop production, the wild food production is negligible (Figure 5f). In the Baltic countries and Belarus, we observe, however, considerable areas with both crop production and wild food production.

Regulating service supply (Figure 5b) is high in the eastern Ukraine and low in the western Bulgaria, Baltic countries and the Carpathian Mountains (Figure 1b and c). In the eastern Ukraine, all regulating ESSs are supplied whereas in most of the other regions our results show a

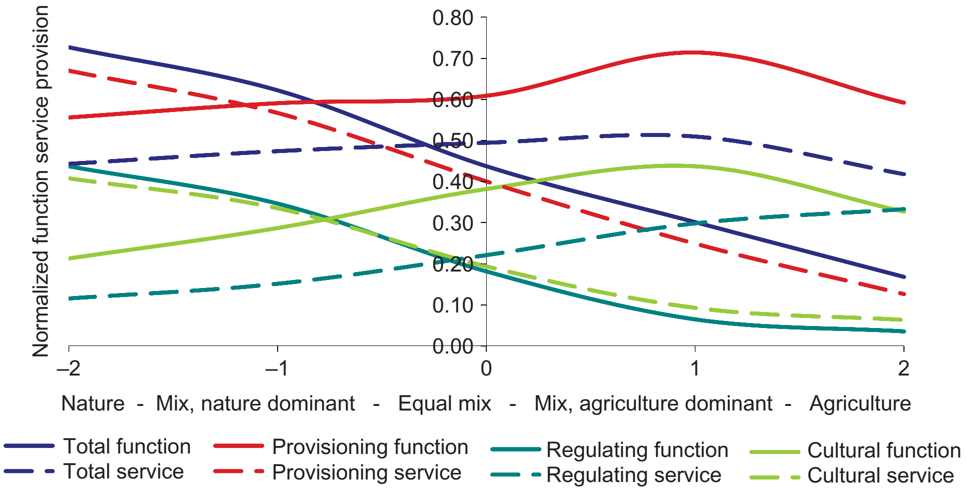

Figure 4. Availability of ecosystem functions and supply of ecosystem services versus the degree of mixing of the land cover.

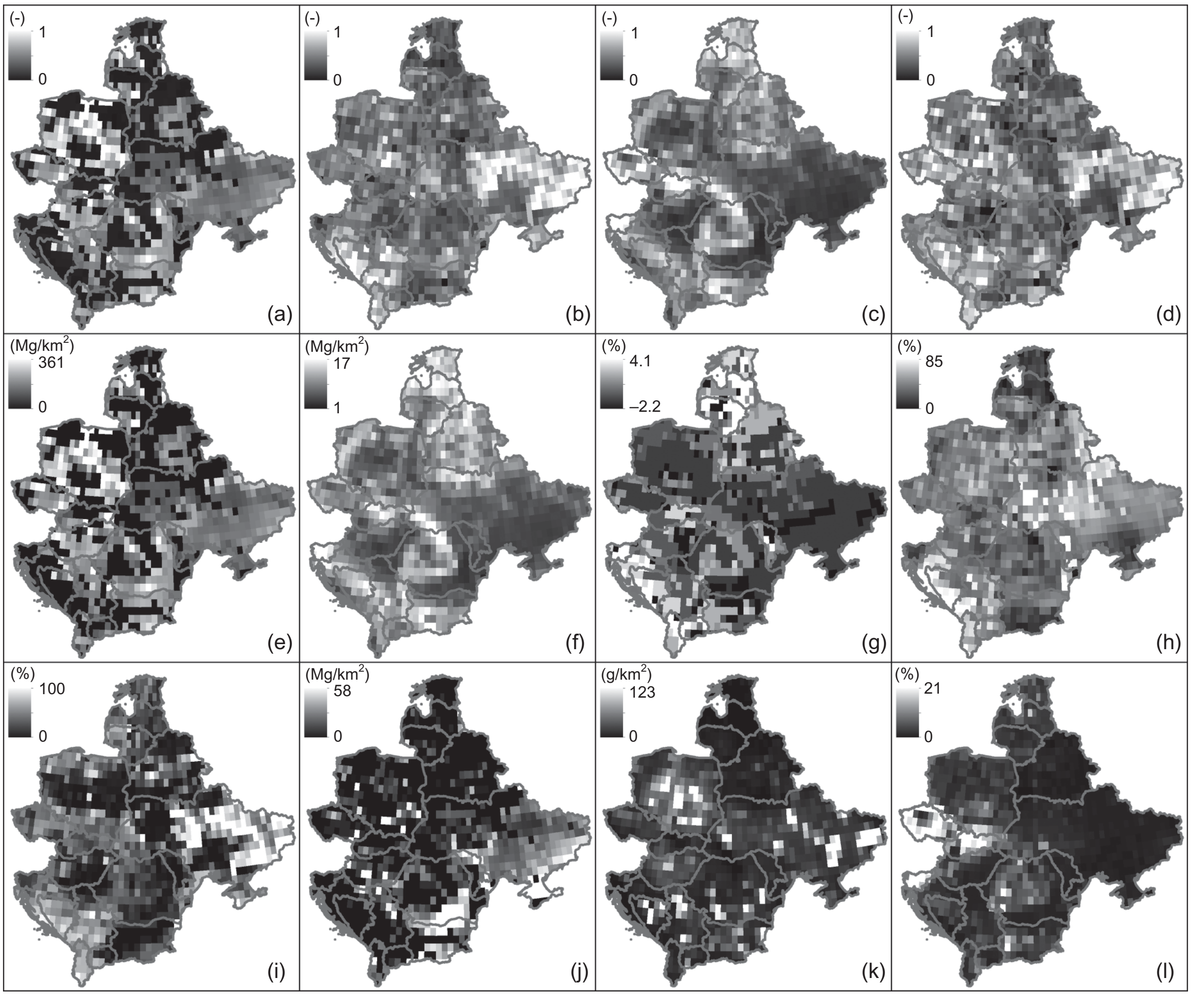

Figure 5. Supply of ecosystem services in Eastern Europe. (a) Normalized sum of provisioning services. (b) Normalized sum of regulating services. (c) Normalized sum of cultural services. (d) Normalized sum of all services. (e) Actual annual food crop yield. (f) Actual annual wild food harvest. (g) Percentage of countries' CO_2 emission captured (negative values are emissions). (h) Erosion protection. (i) Flood protection. (j) Extra annual yield due to good pollination. (k) Annual amount of PM_{10} captured. (l) Landscape attractiveness and accessibility for tourism.

Table 3. Correlations between the supply of different categories of services.

	Cultural services	Provisioning services
Provisioning services	−0.38	
Regulating services	−0.34	0.07

varying pattern of supply of the separate regulating ESSs (Figure 5g–k).

Cultural services (Figure 5c) are mostly supplied in Czech, Slovakia and Slovenia. Wild food collection is mainly done in the Baltic countries and in the mountains (Figure 5f), while parts of Romania are of interest for nature-based tourism (Figure 5l).

As summarized in Figure 5d, the supply of ESSs is highest in Ukraine, mainly because we expect a high supply of the regulating services. Overall, ESS supply is highest in areas with a mixed land cover dominated by agriculture. Supply of provisioning services is highest in uniform agricultural landscapes, while the supply of cultural services decreases with an increasing percentage of agriculture (Figure 4). The supply of regulating services is positively correlated with the percentage agricultural land and the supply of cultural services is positively correlated with the percentage of nature (Table 2). There is little overlap between the three categories of services (Table 3).

ESF availability versus ESS supply

Overall, the patterns of ESF availability and ESS supply do not overlap (Figures 3d and 5d), which is also indicated by the negative correlation (Table 4). While overall ESF availability is highest in areas of uniform natural land cover, ESS supply is slightly higher in areas with mixed land dominated by agriculture (Figure 4). If the three categories of services are considered separately, only for the category of cultural services areas of high ESF availability overlap with areas of high ESS supply, resulting in high correlation (Table 4). For provisioning services, the crop yield function and service lack overlap, while for wild food the overlap is very high. Each regulating service separately follows the overall pattern.

Table 4. Correlation between ESF availability and ESS supply for each service and category of services.

Service	*r*
Overall	0.12
Provisioning	0.21
Regulating	−0.02
Cultural	0.95
Crop yield	0.21
Wild food	0.98
Carbon sequestration	0.47
Erosion risk mitigation	0.18
Flood risk mitigation	0.79
Pollination	0.03
Air quality	−0.27
Tourism	0.82

Discussion

Interpretation of the results

Ecosystem functions

The patterns of ESF availability throughout the study area (Figure 3) are mostly controlled by the land cover. This is imposed by the model input: For many ESFs, land cover is an important driver and especially natural land-cover types have a high functionality. For example, forests are more efficient in capturing dust particles than croplands (Oosterbaan et al. 2006), and natural land cover provides better habitat for wild pollinators and wild food species (Kleijn and van Langevelde 2006; Sharp and Wollscheid 2009) and provide more protection against erosion (Kirkby et al. 2008). Also, natural land cover sequesters more carbon (Schulp et al. 2008) and retains more run-off (Fohrer et al. 2005). Consequently, ESF availability is concentrated in the natural areas of the Carpathian and Adriatic Mountains, in the Prypjat swamps and the Baltic countries. The uniform cropland areas (Hungary, Ukraine, Poland, Romania; Table 2; Figure 1b and c) are low in ESF availability.

For several functions, soil properties, relief and climate are important. For air quality, the lower capture capacity in the Adriatic coast compared to the Baltic Countries (Figure 3k) is due to the differences in temperature and wet day frequency. For flood protection, areas along the Danube and Dnjepr (Figure 1c) with a low flood protection ESF are dominated by soils with a low retention capacity, and are in a landscape position that receives run-off from the surrounding mountains. Relief is an important driver for the high tourism ESF as well. Mainly in Czech and Slovakia, the foothills of the western Carpathian Mountains are attractive for nature tourism (Hall 2000).

The food crop yield ESF is dominantly controlled by climate and soil, while the effect of natural land cover is especially important for regulating and cultural functions. Natural land cover dominantly occurs on locations less favourable for agricultural production and therefore, the hotspots of provisioning functions are spatially separated from the hotspots of regulating and cultural functions. As regulating and cultural functions are controlled in a similar way by the same drivers, they are more clustered.

From functions to services

We mapped ESSs as the use of ESFs by humans using spatial data on human impact. Consequently, ESS supply is clustered in areas utilized for crop production and populated areas. For provisioning services, the areas of function availability (Figure 3e) are evenly spread over the study area, while the crop production ESS (Figure 5e) is concentrated in agricultural areas (positively correlated with the percentage agricultural land; Table 3). Production is highest in the EU member states (Figure 1) because of the higher intensity of agricultural land use in the EU (Donald et al. 2001). However, because of the demand for specific food crops, not always the highest yielding crop may be grown in certain locations. For wild food, remote areas are not utilized for hunting or gathering. Especially, parts of the Carpathian Mountains are too remote to actually supply wild food. In Estonia, the complete country is accessible and the wild food ESF is completely utilized.

For regulating services, the Carpathian Mountains are low in ESS supply (Figure 5b) because the area is unsuitable for crop production and living, due to soil and relief conditions. Air quality regulation is highest in green areas while PM_{10} is emitted in areas with a high road density, close to cities, and in bare areas. Consequently, the ESS for air quality is high in Poland, where a reasonable capture capacity (Figure 3k) is combined with high PM_{10} emissions, mainly from roads and industries (European Environment Agency 2011).

Carbon is sequestered by forests and grasslands. The Baltic and Adriatic countries have low carbon emissions from traffic, industries and other sources (UNstats 2011), while the land cover is dominated by nature, resulting in a relatively large proportion of the countries' emission captured by the ecosystem (Figure 5g). Slovakia, Romania and Ukraine have high greenhouse gas emissions. Despite the large area of nature in these countries, we expect a limited contribution of the land cover to the countries' greenhouse gas balance. The ESS for erosion risk is highest along the Adriatic coast (Figures 3h and 5h). This region combines a high level of erosion protection (Figure 3h) with a high sensitivity for erosion due to the slopes, sensitive soils and erosive rainfall combined with intensive use of the region by humans. In the south of Ukraine, the high erosion protection ESF due to the vegetation structure is not used because the landscape is less sensitive, the rainfall induces less erosion and the production and population density are lower. Pollination is most effective in Belarus because here crops that depend on wild pollinators dominate the agricultural production, while the landscape provides habitat for the pollinators.

For cultural services, there is a slight shift of hotspots from areas dominated by nature where functions are available to areas with more agricultural land where services are supplied (Figures 3l, 4 and 5l). This is due to the higher GDP in Czech and Slovenia (Nowaczek and Fennel 2002). Further, an interesting countryside with relief as is present in Romania, Bulgaria is favoured (Hall 2000), just as the nature parks in Estonia (Eurostat 2011).

Comparison with other studies

To get an impression of the credibility of the results, we compared the ESF and ESS model outputs with other data on the services. In most of the study area, no specific studies on the spatial patterns of ESFs and ESSs are available (Seppelt et al. 2011). Several data sources and studies have been used for comparison.

Food crop yield and carbon sequestration were simulated with IMAGE. Such simulation results are used in numerous global change impact assessments (United Nations Environment Programme 2007; Organisation for Economic Co-operation and Development 2008; The Economics of Ecosystems and Biodiversity 2009) and represent state-of-the-art knowledge on the functioning of the global carbon cycle.

Gallai et al. (2009) estimate the economic value of insect pollinators in Europe at approximately 10% of the total economic value of agricultural production. For the study area, the total crop yield is 157 million ton while the extra yield due to good pollination is estimated to be 10 million ton (6%). This is lower than the 10% given by Gallai et al. (2009), which can be explained by the limited number of crops that depend on pollinators included in the IMAGE model.

The flood protection ESF map was compared with a flood-risk map in the EU member states (Barredo et al. 2007). Areas with a low flood regulation ESF (Figure 3i), such as eastern Hungary, eastern Romania and parts of Poland, Lithuania and Czech, match the areas of high flood risk from Barredo et al. (2007).

To assess the credibility of the nature tourism map, destinations of birding holidays to Eastern Europe offered via the website of Birdlife Netherlands (Vogelbescherming 2011) were inventoried. The bird travels have a preference for the Danube Delta, Estonia and Bulgaria (Figure 1b and c). The areas where we expect a high tourism ESS match these areas. The high tourism ESS in the Carpathian Mountains is not reflected in the supply of bird travels. These areas are probably interesting because of the scenery and the possibilities for walking (Hall 2000).

The erosion ESS map was compared with global-scale NPP changes between 1981 and 2003, where NPP decreases can be interpreted as degradation due to erosion (Bai et al. 2008). Many areas where NPP decrease is observed by Bai et al. (2008) match the areas with a low erosion ESS, for example, southern Ukraine, central Hungary, Estonia, Latvia, Czech and parts of Bulgaria. At locations where NPP increase is observed, the erosion ESS is generally higher. Along the Adriatic coast, Bai et al. (2008) observe NPP loss while we expect a high erosion ESS. This might be due to other processes that cause NPP decrease, or due to erosion processes that cannot be simulated accurately with the USLE, including gully erosion (De Vente et al. 2008). Second, the Adriatic region is highly sensitive to erosion, implying that erosion resulting in NPP loss is likely unless the protective cover.

Methodological issues

The models developed in this study strongly simplify the processes controlling ESF availability and ESS supply. This is due to the data availability combined with the scale of the study. Global-scale data sets have many quality and inconsistency issues, potentially leading to error propagation upon use in ecosystem modelling (Verburg et al. 2011). This also applies for the maps used in this study. Most importantly, the land-cover map is known to have difficulties distinguishing different types of barren land in a case study in the Netherlands (Clevers et al. 2007). Especially in the agriculture-dominated areas in Hungary, Poland and Romania, this could have caused deviations in the results. Although it is difficult to quantify landscape structure at the scale of this study, the land-cover map used in this study provides good insight into the landscape patterns (Kaptué Tchuenté et al. 2011) and has been used with accurate results for mapping the pollination ESF (Schulp and Alkemade 2011). Second, for the applicability at continental or global scale, models need to describe processes controlling ESF and ESS provision in a generic way to match the scale of the processes and the quality of the available data. To limit the consequences of data uncertainties as much as possible, we used the best global-scale data available. Unless the uncertainties and errors in the data, model results provide a reasonable reproduction of the spatial patterns of ESF availability and ESS supply, as demonstrated in Section *Comparison with other studies*.

Next to the generic data requirements, there are data-related issues to the specific models. Several processes explaining ESF availability and ESS supply are not included because of the lack of data. This applies for the effects of wind on PM_{10} capturing (Anttila and Salmi 2006; Vanderstraeten et al. 2008). In the pollination model, several fruit and vegetable species that depend on wild pollinators are not included because of the lack of spatial data. This could result in the underestimation of the importance of pollination when the results are translated into economic outputs. Also for wild food, our results might underestimate the actual harvest. We used official national and international statistics, where illegal harvest is not included. Illegal harvest can comprise a considerable volume compared to the statistics (Muth and Bowe 1998; Kecse-Nagy et al. 2006; Bell et al. 2007). The flood-risk ESF model identifies all areas where floods occur. In many situations, the occurrence of floods is, however, not a risk but a condition for the ecosystem to function. This is, for example, the case in the Prypjat swamps (Figure 1c). Also, floods can also provide irrigation water that is essential for crop production.

Finally, we have modelled each service at the resolution of the input data and aggregated the results to $0.5° \times 0.5°$. Consequently, extreme values have been averaged out and at the input resolution the overlap and correlations between services or groups of services might be lower (Overmars et al. 2003).

Applications

The models developed in this study are, in principle, ready for global-scale use as the model inputs are derived from global-scale data and model outputs (Table 2), and the models are based on generic processes that describe ESF and ESS provision. In Eastern Europe, the models result in credible maps of the spatial patterns of ESF supply and ESS availability. Although the case study area does not comprise the complete range of biophysical, socio-economic, land-cover, soil and climate conditions that should be covered in a global-scale model, we think that the data and models are suitable for global-scale use. However, as the models are empirically based, for several models the quantification needs to be adapted to global scale. The travel time thresholds in the wild food model, for example, are specific to Eastern European conditions. Also, careful evaluation of model results under divergent situations around the globe is still needed.

Ecosystem model results based on proxies for ESFs and ESSs are sensitive to error propagation when results are combined and would be used as guidelines for management choices (Eigenbrod et al. 2010). The models are targeted for use within the IMAGE framework in scenario studies for assessing potential impact of global change on broad spatial patterns of ESF availability and ESS supply. For this goal, models as developed in this study are suitable (Eigenbrod et al. 2010).

Most services we assessed are landscape services, that is, services that can only be used in situ (Lamarque et al. 2011). For such services, land use and management have different effects on functions and services. Land-use change into a spatial arrangement optimal for ESS supply can decrease the availability of ESFs in the landscape. Management aiming at optimizing economic output leads to a different land-use pattern when compared to the management aiming at a high functionality of the landscape (Polasky et al. 2008; De Groot RS, Alkemade R, et al. 2010). With this, we demonstrate that the distinction between ESFs and ESSs is essential for proper modelling of the impact of global change on human well-being through the functioning of ecosystems.

Although the set of eight ESFs and ESSs that we mapped covers a large and diverse range of ESS models (Seppelt et al. 2011), still a substantial part of the whole set of services is uncovered (MA 2005; The Economics of Ecosystems and Biodiversity 2009). While additional services might be derived from the IMAGE framework combined with the global biodiversity model (GLOBIO) (Bouwman et al. 2006; Alkemade et al. 2009) or from the models presented in this article, several other services require further study on quantification and scale sensitivity upon global-scale simulation. In the category of cultural services, we only mapped tourism and considered wild food collection as a cultural service in our case study. For global-scale mapping and modelling aesthetic, spiritual and educational services, more research is needed on the feasibility of mapping and modelling at scales larger than the landscape scale.

Conclusions and recommendations

We modelled a large and diverse set of ESFs and ESSs for a sample area in Eastern Europe, using global-scale data, focusing on regulating services that depend on the spatial and biophysical structure of the landscape. This is one of the first studies where the cascade ecosystem properties–functions–services are simulated in a spatially explicit manner at continental scale. The models are suitable for combining the impact of land cover, soils, relief and climate on ecosystem functioning and use in integrated assessment studies at global scale.

Although the models are highly generalized, they provide an accurate reproduction of spatial patterns of ESF availability and ESS supply. We demonstrated that there is no spatial overlap between ESFs and ESSs, because ESFs and ESSs represent different aspects of the interaction between humans and the landscape. ESFs are dominantly available in natural areas while ESSs are supplied in mixed landscapes, where both ESFs are available from the natural land cover and used by humans. The definition of model inputs and outputs therefore clearly influences the results. As the impact of land cover and management is different for ESFs and ESSs, a clear distinction needs to be made between functioning and use of ecosystems when the impact of global change on human well-being is assessed.

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